

FORTIPECTEN TAKAHASHII, A RECLINING PECTINID FROM THE PLIOCENE OF NORTH JAPAN

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ABSTRACT. The adaptive morphology and mode of life of a large bizarre pectinid, *Fortipecten takahashii* (Yokoyama) from the Pliocene of north Japan and Sakhalin, were examined mainly from the standpoint of relative growth. In spite of its similarity to some extant species of *Patinopecten* in the early growth stage, *Gryphaea*-like and unusually heavy valves are formed after the middle stage by a drastic change of growth pattern. In the later stage, unlike many swimming pectinids, the weight of the valves becomes positively allometric to the cube of shell size, indicating remarkable relative thickening of the shell. The decrease of umbonal angle, abrupt inward bending of the shell surface, and disappearance of anterodorsal and postero-dorsal gapes also suggest rapid loss of swimming ability in the middle stage. After it escaped from predators in the young stage, this pectinid probably abandoned a swimming strategy and became an immobile recliner on soft substrates. *F. takahashii* is thus regarded as an exceptional Cainozoic bivalve which succeeded, though only temporarily, in resurrecting Mesozoic-type reclining life habits in some inland seas of the north-western Pacific region.

THE diversity of immobile suspension feeders living freely on soft sea-bottoms appears to have declined significantly with geologic time. In the Mesozoic *Gryphaea*, *Exogyra*, and some other coiled oysters were undoubtedly full-time recliners, but after the 'Late Mesozoic marine revolution (Vermeij 1977)' gryphaeid oysters only rarely occupied this niche. *Gryphaea*-like gross morphology is known also in various Mesozoic non-ostreacean bivalves (Carter 1972; Jablonski and Bottjer 1983; Seilacher 1984). In modern seas only a few species of *Placuna* are regarded as recliners (snowshoe strategists), and all other free-living bivalves on soft substrates have escape strategies such as burrowing and swimming. As was interpreted by Stanley (1970), Thayer (1975, 1979), and LaBarbera (1981), the rarity of full-time recliners in the Cainozoic-Recent seas is most certainly due to increased predation pressure as well as increased bioturbation by deposit feeders.

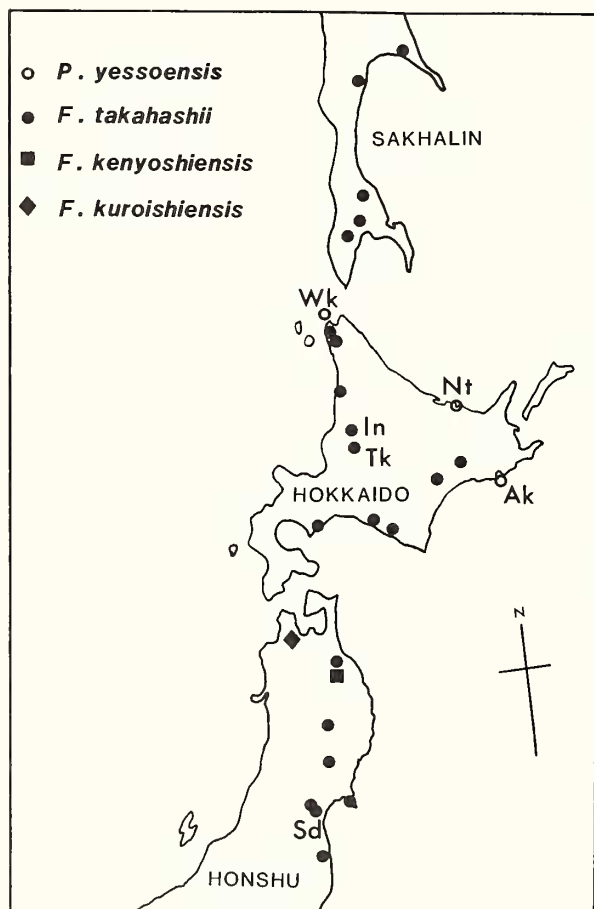
Fortipecten takahashii (Yokoyama, 1930) and its related species from the Pliocene (partly Upper Miocene) of the north-west Pacific region (north Japan, Sakhalin, Kamchatka, and Alaska) reveal *Gryphaea*-like morphology in the adult stage which is characterized by an unusually heavy shell for pectinids and a bowl-like inflated right (lower) valve. From this and some other reasons one of us (I. H.) has long supposed that the adult individuals of these species may have been almost immobile recliners on soft substrates. If this is true, *Fortipecten* can be regarded as a unique bivalve which succeeded in developing such a reclining strategy in the post-Cretaceous seas.

Since *Fortipecten* is a conspicuous and relatively short-ranging taxon (commonly treated as a subgenus of *Patinopecten* or a distinct genus), many authors have investigated its geographic distribution and biostratigraphic significance in addition to making systematic descriptions (see Masuda 1962a, 1978; Kafanov 1986a, b). On the other hand, little has been discussed about the mode of life and the functional significance of its peculiar morphology. In this paper we intend to analyse the morphology of *Fortipecten*, especially its type-species *F. takahashii*, to elucidate the mode of life. Because the young individuals of this species are biconvex and thin-shelled like many swimming species of *Patinopecten*, the analysis of its allometric growth as well as comparative studies with extant free-living pectinids and Mesozoic *Gryphaea*-like homeomorphs will be important for this purpose.

PREVIOUS STUDIES AND GENERAL MORPHOLOGY OF *FORTIPECTEN*

Yokoyama (1930) first described *Pecten takahashii* from the Pliocene beds at Isousi of the Motodomari area, south Sakhalin. *P. agnatus*, which was simultaneously erected by him from the same area, is undoubtedly synonymous, because it is, as was interpreted by Masuda (1962a) and some others, merely an immature specimen of *P. takahashii*. The shell morphology of this pectinid, in fact, changes so greatly with growth that the young specimens look as if they were specifically different from the adult ones. Subsequently the occurrence of *P. takahashii* was recorded from the Pliocene of other areas of Sakhalin (Khomenko 1931, described under the name of *P. pilutunensis*; Kryshstofovich 1964), Kamchatka (Ilyina 1963; Gladenkov 1984), various areas of Hokkaido (Yokoyama 1932; Nomura 1935; Takeuchi and Sanbonsugi 1938; Fujie 1958; Akamatsu *et al.* 1979; Oka and Akamatsu 1979; Uozumi *et al.* 1986), as well as the Pacific side of north Honshu (Nomura 1938; Masuda 1962b; Hayasaka and Hangai 1966; Noda and Masuda 1968). Though considerably wide intrapopulational and geographic variation have been known (Yabe and Hatai 1940; Suzuki 1979), this species is generally characterized by the heavy test, strong convexity of the adult right valve, unusually large auricles, and eleven to seventeen radial costae which are often of two orders of prominence in the adult left valve.

Since Kuroda (1932) assigned *P. takahashii* to *Patinopecten*, many authors have considered that this pectinid should be taxonomically placed in or near that genus. In fact, the young shell of



TEXT-FIG. 1. Geographic distribution of *Fortipecten* in north Japan and south Sakhalin. Localities of studied samples of *Fortipecten takahashii* and *Patinopecten yessoensis* are indicated by symbols.

Pecten takahashii, as shown later in detail, is weakly convex, thin-shelled, and considerably similar to *Patinopecten* (*Mizuhopecten*) *yessoensis* (Jay, 1857), a commercial scallop in the north-western Pacific. Since Yabe and Hatai (1940) proposed the subgenus *Fortipecten* for *Pecten takahashii*, most palaeontologists have regarded it as a valid genus-group name, but some different taxonomic evaluations have been made about the peculiar morphology of this species. For example, Akiyama (1962) regarded the heavy and strongly inflated shell as due to adaptation to some lagoonal environment and denied its subgeneric distinction from *Patinopecten*. In contrast, Masuda (1962a) treated *Fortipecten* as a distinct genus, and furthermore a new subfamily Fortipectininae was proposed (Masuda 1963).

In addition to *Pecten takahashii*, the following species seem to belong to *Fortipecten*, though their diagnostic characters are not necessarily clear:

Pecten (*Plagiectenium*) *hallae* Dall, 1921, from the Pliocene of east Alaska. [? = *P. (Patinopecten) rhytidus* Dall, 1921].

P. mironovi Khomenko, 1934, from the Pliocene of Sakhalin.

P. (P.?) sachalinensis Ilyina, 1957, from the Pliocene of Sakhalin.

P. (Fortipecten) kenyoshiensis Chinzei, 1960, from the Pliocene of north Honshu.

P. (F.) makarovi Kryzhtofovich, 1964, from the Pliocene of Sakhalin.

Fortipecten mollerensis MacNeil, 1967, from the Pliocene or Upper Miocene of south Alaska.

F. kuroishiensis Kotaka and Noda, 1967, from the Upper Miocene of north Honshu.

Because the intrapopulational and geographic variation of each species may be wide, its taxonomic discrimination and phylogenetic relation to other species should be studied at the population level. In this paper we do not discuss this problem, because the examined material is still restricted to several samples from north Japan and south Sakhalin.

A REVIEW OF SUZUKI'S BIOMETRIC STUDY

An elaborate biometric study of *F. takahashii* was carried out by Suzuki (1979). He investigated various characters of the shell (mainly right valve) such as shell height, convexity, surface curvature, weight, and development of each shell layer on the basis of four samples from different areas of Hokkaido, and discussed the mode of shell growth and geographic variation. His data and conclusions seem to be reliable. Because his paper appeared in a special Japanese publication of limited distribution, we review here, with his permission, his important conclusions in the following section.

1. The samples of *F. takahashii* are morphologically classifiable into two forms. Though the variation in each sample is wide, Form A, occurring in the Japan Sea side of Hokkaido (i.e. Takikawa and Ishikari-numata areas) as well as south Sakhalin is characterized by a heavier test and stronger convexity of the right valve than Form B from the Pacific side of Hokkaido (i.e. Tokachi and Akan areas) and north Honshu.

2. The surface of the right valve of *F. takahashii* often bends abruptly inward at the middle growth stage when shell height attains about 70 mm. After this stage the shell becomes much thicker and convexity becomes stronger especially in the samples belonging to Form A. The crook-backed appearance and strong convexity of right valves are mainly attributable to this bending rather than the change of surface curvature.

3. The subvertical section of an adult right valve shows almost uniform robustness of the whole shell which is formed by the much thickened outer layer in the ventral area and the thickly accumulated inner layer in the umbonal area.

Suzuki (1979, text-fig. 4) examined the relation between shell height (H) and weight (W) of right valves in his sample from the Ishikari-numata area which is composed of many well-preserved specimens of various growth stages. His data were plotted again by us on a double logarithmic scatter diagram in order to recognize their allometric relation more clearly. From this diagram

the relation between H and W was recognized as diphasic allometry; that is, in the early growth stages ($H < 70$ mm) W increases nearly in proportion to H^3 , whereas the growth ratio (or the slope of the best-fit in the diagram) in the later growth stages ($H > 70$ mm) is as large as 1.4. Though it may be partly due to the crook-backed shape of right valves, it is strongly suggested that the shell is at first thickened nearly isometrically, and that the heaviness of adult valves is formed by the significant positive allometry of shell thickness to shell size after the middle growth stage. Similar change of the growth pattern was also ascertained in the samples collected by us (see text-fig. 7).

MATERIAL AND EXAMINED CHARACTERS

In order to elucidate the adaptive significance of the peculiar morphology of *F. takahashii*, the relative growth of the shell was analysed on the basis of the following samples (articulated, right and left valves are indicated by CV, RV, and LV, respectively, and observed ranges of length (L), height (H), and weight (W) are shown in parentheses).

Sample In [UMUT CM18116]. 25CV ($L = 34.3\text{--}147.0$ mm, $H = 35.4\text{--}154.9$ mm, $W = 3.37\text{--}600.14$ g), 152RV ($L = 13.0\text{--}137.0$ mm, $H = 13.0\text{--}146.5$ mm, $W = 0.12\text{--}284.08$ g), and 151LV ($L = 12.2\text{--}133.9$ mm, $H = 12.3\text{--}136.6$ mm, $W = 0.07\text{--}227.25$ g). Locality: Lower Pliocene Horokaoshirika Formation at the river floor of the Horoshintachibetsu, about 3.5 km north-west of Ishikari-numata JR Station, Numata Town, Uryu County, central Hokkaido. This sample contains individuals of various growth stages and suitable for the study of relative growth.

Sample Tk [UMUT CM18117]. 22CV ($L = 63.2\text{--}170.6$ mm, $H = 62.9\text{--}169.5$ mm, $W = 19.23\text{--}707.88$ g), 38RV ($L = 22.3\text{--}159.5$ mm, $H = 23.0\text{--}164.0$ mm, $W = 1.22\text{--}422.99$ g), and 49LV ($L = 44.5\text{--}159.5$ mm, $H = 48.0\text{--}152.0$ mm, $W = 3.43\text{--}364.25$ g). Locality: Lower Pliocene Takikawa Formation at the river floor of the Sorachi, East 2-chome of Takikawa City, about 4 km east of Takikawa JR Station, central Hokkaido (partly collected by Y. Iwasaki). Most specimens are well-preserved adult individuals.

Sample Sd [UMUT CM18118]. 5CV ($L = 102.0\text{--}161.2$ mm, $H = 98.9\text{--}164.0$ mm), 4RV ($L = 126.1\text{--}160.2$ mm, $H = 121.4\text{--}154.5$ mm), and 7LV ($L = 84.5\text{--}150.5$ mm, $H = 80.8\text{--}144.1$ mm). Locality: Lower Pliocene Tatsunokuchi Formation near Yodomibashi Bridge, Sendai City, Miyagi Prefecture. Though the sample size is small, this is the best-preserved sample from the Pacific side.

The relative growth of a living species, *Patinopecten yessoensis*, was also examined and compared with that of *F. takahashii* on the basis of the following samples.

Sample Ak [UMUT RM18119]. 49CV ($L = 18.2\text{--}165.8$ mm, $H = 17.6\text{--}160.9$ mm, $W = 0.39\text{--}265.18$ g). Locality: Akkeshi Bay, off Akkeshi Town, Kushiro County, eastern Hokkaido.

Sample Nt [UMUT RM18120]. 131CV ($L = 15.4\text{--}146.5$ mm, $H = 15.9\text{--}144.4$ mm, $W = 0.14\text{--}180.11$ g). Locality: Noto Estuarine Lake, near Abashiri City, northern Hokkaido. In spite of the large sample size, this sample is not necessarily ideal, because most of the specimens are probably cultivated individuals. The shell is often abnormally thin and sometimes distorted.

Sample Wk [UMUT RM18121]. 14CV ($L = 122.5\text{--}192.1$ mm, $H = 118.7\text{--}173.5$ mm, $W = 113.58\text{--}331.00$ g). Locality: Soya Strait, off Wakkanai City, northern Hokkaido. This sample represents only the later growth stages.

Various morphological terms relating to pectinid valves in this study are adapted mainly from those defined by Waller (1969). We examined various linear measurements, angles, and weight of these specimens. Among others, the following measurements are useful because their interrelations indicate allometric change of shell form.

L : Maximum length of disc, measured in the direction parallel to outer ligament (or hinge axis).

H : Distance between the origin of growth and the most ventral point of the valve, measured in the direction perpendicular to outer ligament.

D : Length of outer ligament, which also represents the total length of the two auricles.

T : Maximum thickness of articulated valves (in closed condition), measured in the direction perpendicular to commissure plane.

U: Umbonal angle (in degrees) between two lines from the origin of growth to the anterodorsal and posterodorsal shoulders of disc, as was defined by Stanley (1970, p. 20). Only left valves were used.

W: Weight of a valve (or articulated valves).

Computations for statistics were made separately on each valve excluding some broken specimens which were inadequate for measurement. Besides, the extent of anterodorsal and posterodorsal gapes, marginal discrepancy of discs, symmetry of disc, surface curvature, spiral angle in vertical section, and size, position, and obliquity of striated (quick) and smooth (slow) adductor muscles may be intimately related to the difference of life habit. These characters were, though mostly qualitatively, examined and evaluated at need. All the specimens used in this study are preserved in the University Museum, University of Tokyo (UMUT).

ALLOMETRIC CHANGE OF SHELL FORM

As vigorously discussed by Gould (1971), isometric (proportional) growth of pectinid valves would result in the decline of swimming ability, because the gravitational force scales at the cube of the length (L^3) while the lifting force scales at smaller powers of the length (generally supposed as L^2 , provided that the swimming velocity is independent of shell size). In order to maintain swimming ability, many free-living pectinids appear to undergo various allometric changes especially in the later growth stages.

In the early growth stages *F. takahashii* and *P. yessoensis* share various characteristics, e.g. thin and subequiconvex valves, simply rounded radial costae, shagreen microsculpture on the left valve, and distinct anterodorsal and posterodorsal gapes between discs. As commonly recognized in many extant free-living scallops, the early dissoconchs of *F. takahashii* and *P. yessoensis* possess several denticles of active ctenolium along the anterodorsal margin of the right disc, which indicate the presence of a byssate stage before the free-living stage. The general morphological similarity seems to suggest that the mode of life in the early growth stages is nearly identical between the two species.

The peculiar *Gryphaea*-like outline and heavy test formed in the later stages of *F. takahashii*, as demonstrated by Suzuki (1979), are largely attributable to the highly allometric growth after the middle stage when the shell height (or length) attains about 70 mm. The change of growth pattern at this size is drastic enough to assume some significant change in the mode of life. In *P. yessoensis* the outline of the shell also changes from subequiconvex to right-convex, but no critical change of growth pattern is perceptible. The shell appears to grow nearly isometrically or slightly allometrically until the latest growth stage.

In the following section we describe the relative growth of these two pectinids by means of current bivariate methods (the results are collectively shown in Table 1) and discuss the adaptive significance of the differences.

Shell elongation and umbonal angle

The ventral elongation of pectinid discs (or the ratio of height/length) seems to be inversely correlated to the umbonal angle. Stanley (1970) pointed out that free-living pectinids are generally characterized by a broader (lower) shell and a larger umbonal angle than byssate pectinids. He interpreted that a large umbonal angle is advantageous for swimming motion, because the currents expelled from the gapes of anterodorsal and posterodorsal margins pass more directly in a dorsal direction, so that the resultant propelling force is increased. Moreover, by analogy with a hydrofoil, the broader disc (or smaller ratio of height/length) must produce a greater ratio of lift/drag (Kármán and Burgers 1963).

We examined the relationship between the umbonal angle (*U*) and shell height (*H*) through the growth of *F. takahashii* and *P. yessoensis*. As shown in text-fig. 2, the mean umbonal angle is nearly the same in the early growth stages of the two species, but ontogenetically it becomes smaller in *F. takahashii* and larger in *P. yessoensis*. Owing to the wide intrapopulational variation

TABLE 1. Bivariate analyses for the recognition of allometric growth. a , σ_a , and b : slope, its standard error and Y -intercept of the best-fit (reduced major axis, $Y = aX + b$), respectively.

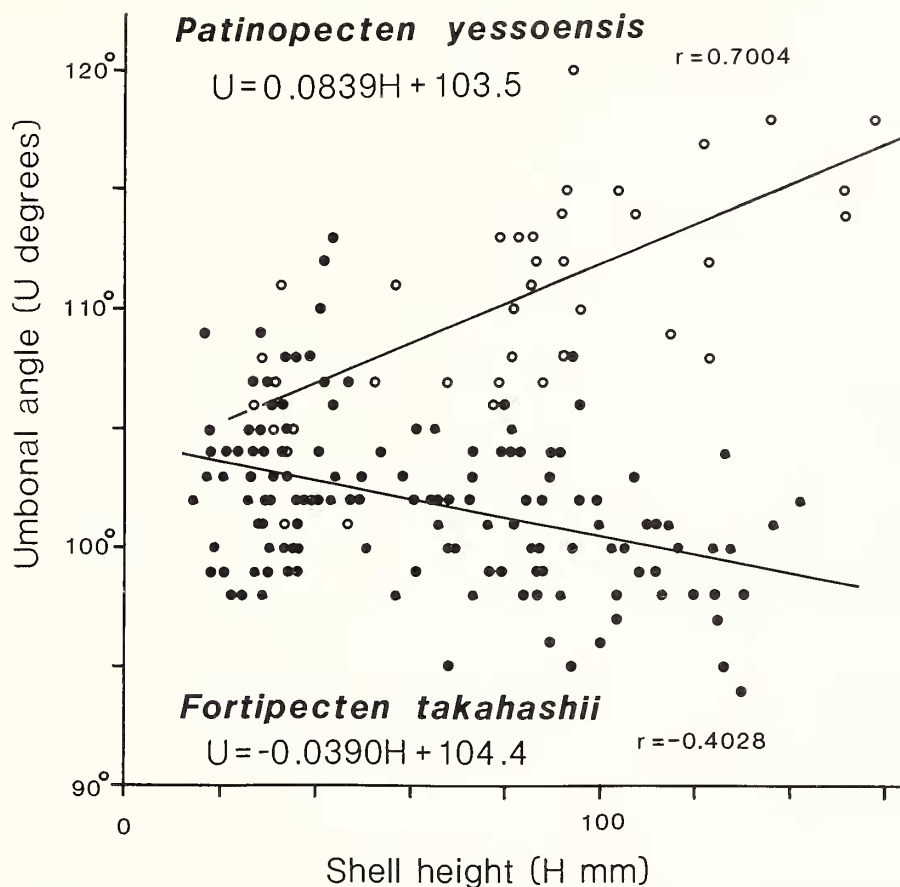
Species	Sample	Valve	Size	X	Y	N	r	a	σ_a	b
<i>F. takahashii</i>	In	RV	All	Log L	Log H	159	0.9979	1.003	0.005	1.002
	In	RV	All	Log L	Log D	81	0.9945	1.150	0.013	0.390
	In	RV	$H > 70$	Log H	Log W	57	0.9739	4.148	0.125	3.878×10^{-7}
	In	RV	$H < 70$	Log H	Log W	81	0.9881	3.025	0.052	4.429×10^{-5}
	In	LV	All	Log L	Log H	152	0.9988	0.978	0.004	1.114
	In	LV	All	Log L	Log D	65	0.9933	1.189	0.017	0.349
	In	LV	$H > 70$	Log H	Log W	55	0.9678	3.749	0.127	2.384×10^{-6}
	In	LV	$H < 70$	Log H	Log W	80	0.9888	3.081	0.051	3.514×10^{-5}
	In	CV	All	Log H	Log T	23	0.9825	1.380	0.054	6.950×10^{-2}
	Tk	RV	All	Log L	Log H	56	0.9906	1.025	0.019	0.908
	Tk	RV	All	Log L	Log D	35	0.9526	1.156	0.059	0.354
	Tk	RV	$H > 70$	Log H	Log W	35	0.9672	4.100	0.176	4.519×10^{-7}
	Tk	LV	All	Log L	Log H	68	0.9928	1.010	0.015	0.976
	Tk	LV	All	Log L	Log D	32	0.9703	1.172	0.050	0.353
	Tk	LV	$H > 70$	Log H	Log W	46	0.9612	3.749	0.152	2.512×10^{-6}
	Tk	CV	All	Log H	Log T	22	0.9093	1.917	0.170	4.887×10^{-3}
<i>P. yessoensis</i>	Ak	RV	All	Log L	Log H	49	0.9989	0.999	0.007	0.986
	Ak	RV	All	Log L	Log D	41	0.9960	0.996	0.014	0.542
	Ak	RV	$H > 90$	Log H	Log W	19	0.9656	2.937	0.175	4.743×10^{-5}
	Ak	RV	$H < 90$	Log H	Log W	30	0.9953	3.188	0.056	1.691×10^{-5}
	Ak	LV	All	Log L	Log H	49	0.9989	0.992	0.007	1.029
	Ak	LV	All	Log L	Log D	43	0.9955	0.991	0.014	0.564
	Ak	LV	$H > 90$	Log H	Log W	19	0.9777	2.778	0.134	9.861×10^{-5}
	Ak	LV	$H < 90$	Log H	Log W	30	0.9952	3.218	0.057	1.538×10^{-5}
	Ak	CV	All	Log H	Log T	48	0.9903	1.009	0.020	0.256
	Wk	RV	All	Log L	Log H	13	0.9841	0.846	0.042	2.077
	Wk	RV	All	Log L	Log D	11	0.9756	1.088	0.072	0.332
	Wk	RV	All	Log H	Log W	13	0.9682	2.774	0.192	1.016×10^{-4}
	Wk	LV	All	Log L	Log H	14	0.9879	0.880	0.036	1.777
	Wk	LV	All	Log L	Log D	13	0.9103	1.210	0.139	0.186
	Wk	LV	All	Log H	Log W	14	0.9389	3.012	0.277	2.825×10^{-5}
	Wk	CV	All	Log H	Log T	13	0.9357	0.828	0.081	0.596

the absolute values of the correlation coefficient (r) between H and U are not high (0.4028 in *F. takahashii* and 0.7004 in *P. yessoensis*), but the correlations are certainly significant with 99.9 % confidence. The ontogenetic enlargement of the umbonal angle is certainly effective in reducing difficulty of swimming. In other words the growth pattern of *P. yessoensis* is normal for swimming pectinids, but that of *F. takahashii* is quite abnormal.

The ontogenetic change of shell elongation can be quantified by the relative growth of the height (H) to the length (L). The reduced major axes on double logarithmic scatter diagrams (not illustrated here) indicate that in both species H increases nearly isometrically to L . We could not detect any statistically significant difference between the growth ratios of the most suitable samples In and Ak. It must be noted, however, that the growth patterns of the two species become considerably different toward the latest stage, because the growth ratios in the adult-rich samples of the two species differ significantly from each other (1.025 ± 0.019 in Sample Tk, and 0.846 ± 0.042 in Sample Wk). We often encountered very tall adult individuals of *F. takahashii* in which H is much larger than L . Such a large form ratio is never found in the adult specimens of *P. yessoensis* and other extant pectinids with adept swimming ability.

Development of auricles

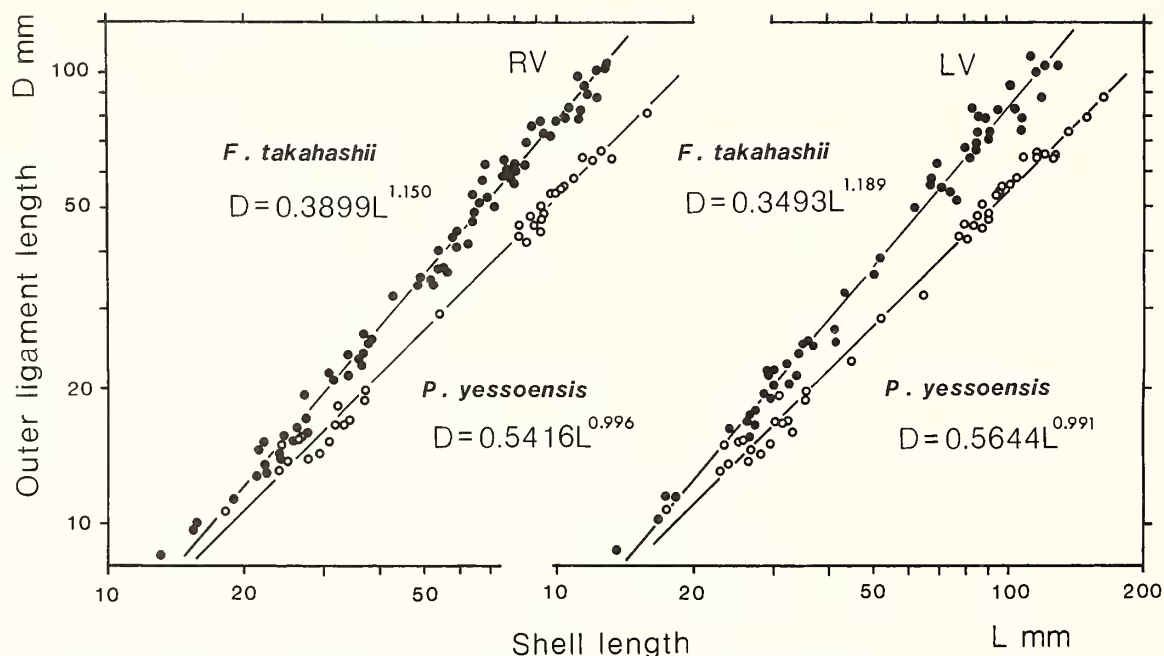
The anterior and posterior auricles of *F. takahashii* are unusually large. This is generally regarded as a diagnostic character of the genus *Fortipecten* (Masuda 1962a; Hertlein in Cox *et al.* 1969;



TEXT-FIG. 2. Relation between shell size and umbonal angle. The umbonal angle becomes larger with growth in *Patinopecten yessoensis* (as in many other swimming pectinids) but smaller in *Fortipecten takahashii*. The left valves of samples Ak and In were analysed. The absolute values of r are not high, but the correlations are very significant ($P < 0.001$).

Kafanov 1986b). The ontogenetic change of the auricular development can be roughly shown by the relative growth of the length of outer ligament (D) to the overall length of disc (L). As shown in text-fig. 3, the reduced major axes signify that D is nearly isometrically increased to L in *P. yessoensis*, but that the relative growth is decidedly positively allometric in *F. takahashii*. The calculated growth ratios (slope of reduced major axis) in the latter species (Sample In) is 1.150 ± 0.013 for the right valve and 1.189 ± 0.017 for the left valve. *F. takahashii* possesses somewhat larger auricles than *P. yessoensis* even in early growth stages, and the difference becomes more striking with growth. Because nearly isometric or negatively allometric growth of auricles is commonly seen in ordinary pectinids (both byssate and free-living), the growth pattern of *F. takahashii* must be said to be unusual.

The functional meaning of auricles in non-byssate pectinids is poorly known, but the symmetry of auricles may be required for swimming straight forward. The large auricles of *F. takahashii* may be useful for a reclining life, because they probably stabilize the horizontal living attitude on soft substrates.



TEXT-FIG. 3. Allometric relation between shell length (L) and outer ligament length (D). The unusually large auricles of *Fortipecten takahashii* are the product of a positively allometric growth of D against L . The samples In and Ak were analysed.

Marginal discrepancy of discs

Marginal discrepancy of discs is generally insignificant in byssate pectinids, but the right (lower) valve is often somewhat larger and overlaps the ventral margin of the left (upper) valve in right-convex free-living genera (e.g. *Pecten*, *Euvola*, and *Patinopecten*). The degree of discrepancy varies among species but generally seems to relate to the convexity of the right valve. Both in *P. yessoensis* and *F. takahashii* the discrepancy is small in the early growth stages and becomes gradually larger with growth. Though the marginal part of the right valve is apt to be broken in articulated specimens of *F. takahashii*, the discrepancy sometimes exceeds 10 mm in the latest stage.

Considering the life habits of plano-convex free-living pectinids (Stanley 1970; our observations in aquaria), the overlapping ventral margin of the lower valve appears to be effective in permitting a horizontal and half-buried living attitude without clogging so that only the tentacled mantle margin is exposed above the soft substrate. In plano-convex immobile recliners this feature may be similarly efficient in permitting cleansing of the mantle cavity.

Anterodorsal and posterodorsal gapes

It has been noticed that many free-living pectinids with an adept swimming habit are characterized by the development of gapes along the anterodorsal and posterodorsal margins of discs (Waller 1969; Stanley 1970; and others). Such gapes are generally undeveloped in byssate pectinids, though in a few species (e.g. *Aequipecten opercularis*) this feature coexists with an active ctenolium which indicates the presence of a byssus. The gapes seem to be effective in swimming because the animal can expel jet currents through them.

The young individuals of *P. yessoensis* and *F. takahashii* are similarly characterized by narrow but distinct anterodorsal and posterodorsal gapes. The gapes are maintained throughout growth and are somewhat widened toward the later growth stages in *P. yessoensis*, whereas the anterodorsal

and posterodorsal margins are almost closed after the middle growth stage in *F. takahashii* (Pl. 39, fig. 1c, d). The disappearance of gapes seems to occur immediately after the change of growth pattern when the shell size attains about 70 mm in length. The size of gapes does not seem to be proportionate to swimming ability, but their disappearance in the middle stage of *F. takahashii* indicates a loss of swimming ability. For reclining life such gapes must be unnecessary and rather disadvantageous.

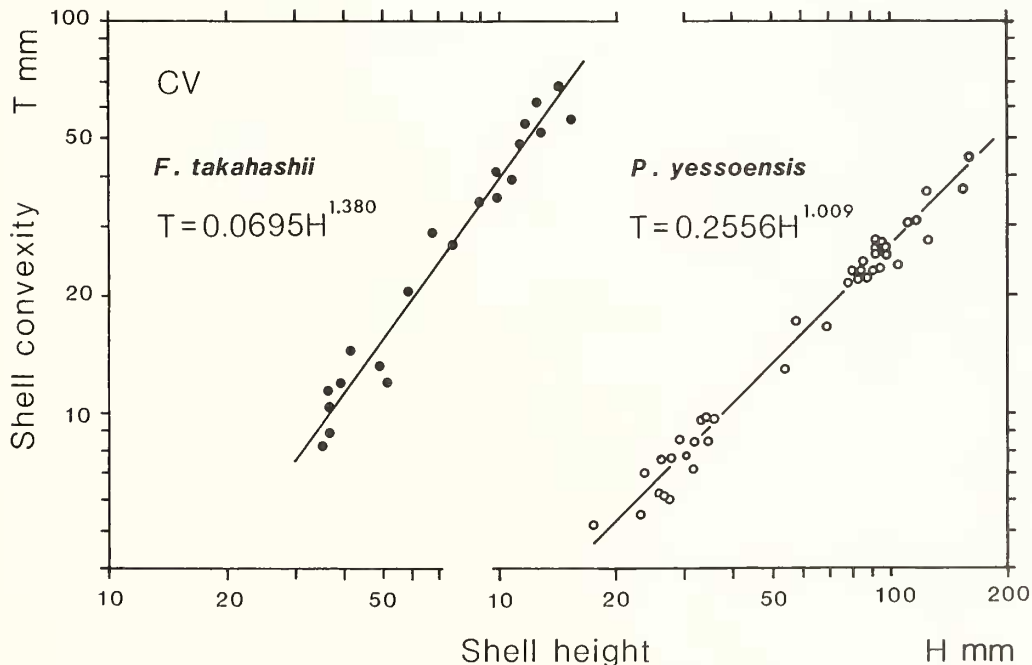
Symmetry of disc

The disc of *F. takahashii*, unlike *P. yessoensis* and many other swimming pectinids, is commonly asymmetric with a more or less prosoclinal demarcation line. The obliquity is as large as 15° in some specimens (e.g. UMUT CM 18117b; Pl. 40, fig. 3a). Such an asymmetric disc is probably disadvantageous for swimming motion and has never been observed in *P. yessoensis* and other adept swimming pectinids.

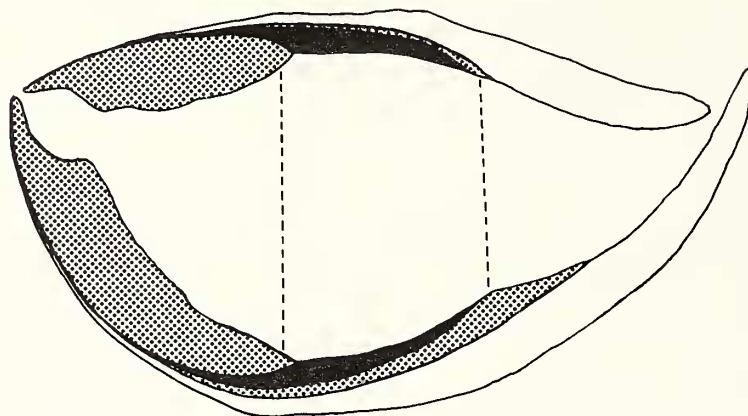
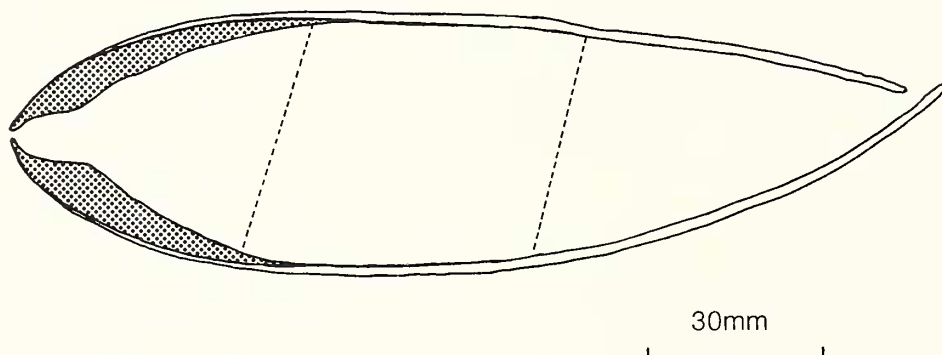
Shell convexity

The relation of shell convexity to swimming ability in pectinids has been discussed by some authors (see Waller 1969). Judging from the great variability of shell form of swimming species involving left-convex, equiconvex, right-convex, and concavo-convex, the mode and extent of shell convexity are not necessarily decisive factors for swimming, even though they are intimately related to swimming orientations (Waller 1969; Stanley 1970).

The convexity of a pectinid valve, especially that of *F. takahashii*, is somewhat difficult to quantify with accuracy, because the commissure of both valves does not lie within one plane. Therefore, we analysed the allometric relation between shell height (H) and maximum convexity (T) in articulated individuals (in closed condition). As shown in text-fig. 4, the relative growth



TEXT-FIG. 4. Allometric relation between shell height (H) and shell convexity (T) in articulated specimens (in closed condition). The relative growth is nearly isometric in *Patinopecten yessoensis* (Sample Ak), but T is highly positively allometric against H in *Fortipecten takahashii* (Sample In).

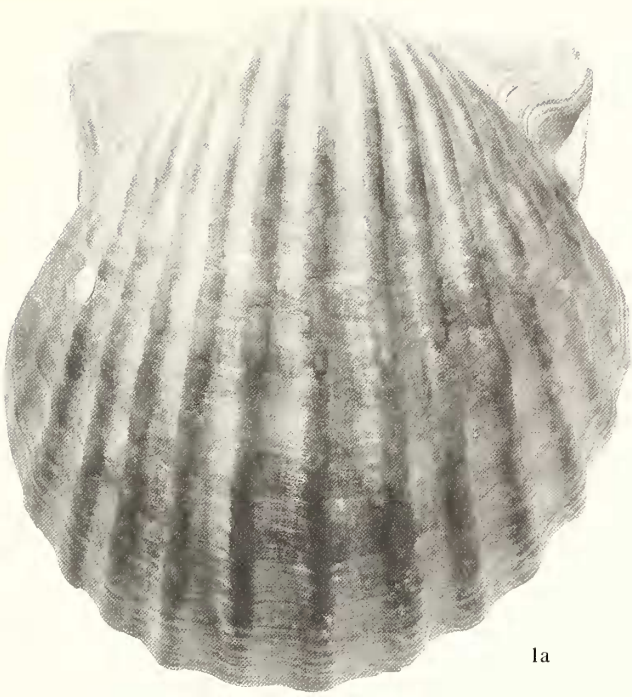
Fortipecten takahashii*Patinopecten yessoensis*

TEXT-FIG. 5. Subvertical sections of full-grown valves of *Fortipecten takahashii* (UMUT CM18117c) and *Patinopecten yessoensis* (UMUT RM18119a). Note the thin outer layer in the earlier part and the abrupt thickening of each shell layer in *F. takahashii*. Solid part: myostracum (prismatic aragonite), dotted part: inner shell layer (crossed lamellar aragonite), open part: outer shell layer (foliated calcite), broken lines: projection of the margins of the adductor muscle on the subvertical section.

is nearly isometric in *P. yessoensis* (Sample Ak) but positively allometric in *F. takahashii* (Sample In). If only large specimens are considered, the growth ratio of the latter species, as shown by the Sample Tk, is as large as 1.9. Because the convexity of the left valve is generally weak throughout growth, the highly allometric nature is largely attributable to ontogenetic change of the right valve.

EXPLANATION OF PLATE 39

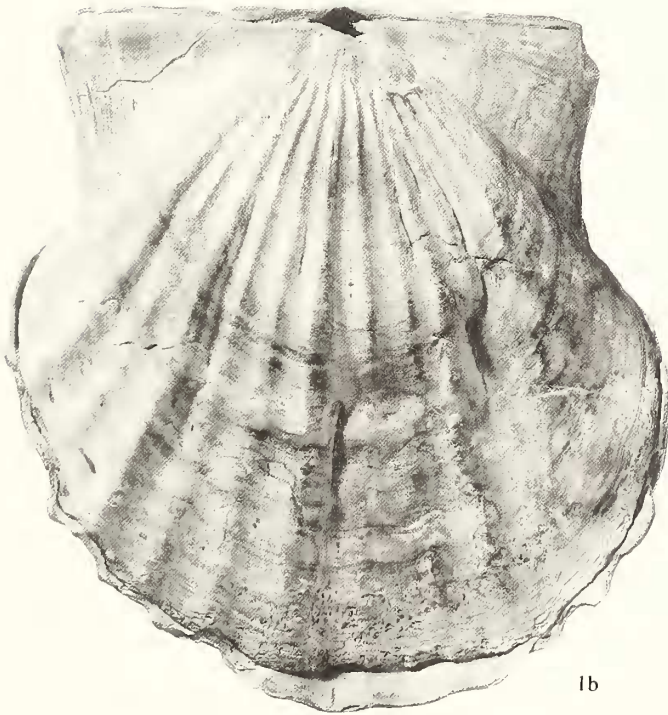
Fig. 1. *Fortipecten takahashii* (Yokoyama, 1930). Full-grown individual, UMUT CM18117a, $\times 0.65$. 1a: right view, 1b: left view, 1c: posterior view, 1d: anterior view. Loc.: Pliocene Takikawa Formation at the river floor of the Sorachi, East 2-chome of Takikawa City, central Hokkaido (collected by Y. Iwasaki).



1a



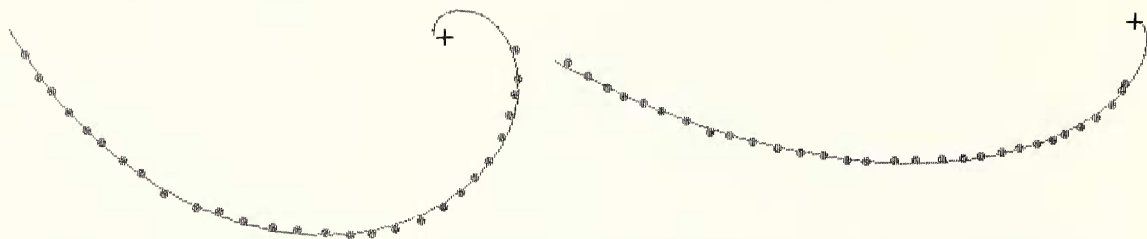
1c



1b



1d

Fortipecten takahashii***Patinopecten yessoensis***

TEXT-FIG. 6. Computer graphics showing the method to obtain the best-fit of an equiangular spiral and its spiral angle. The dots were obtained from an actual specimen along the top of a radial costa near the demarcation line. The spiral angle is about 58° in *Fortipecten takahashii* (UMUT CM18117a) and about 33° in *Patinopecten yessoensis* (UMUT RM18119b). The outer surface of a pectinid valve in the vertical section was approximated by an equiangular spiral lacking the initial part near the origin instead of a spiral with enlarging spiral angle.

In vertical sections of *F. takahashii*, as described by Suzuki (1979) and reconfirmed here (text-fig. 5), there is often a critical bending point at about 70 mm distance from the beak, where the relative convexity begins to increase at an unusually high rate. Such a remarkable ontogenetic change of shell convexity has not been observed in swimming pectinids.

Spiral angle and surface curvature

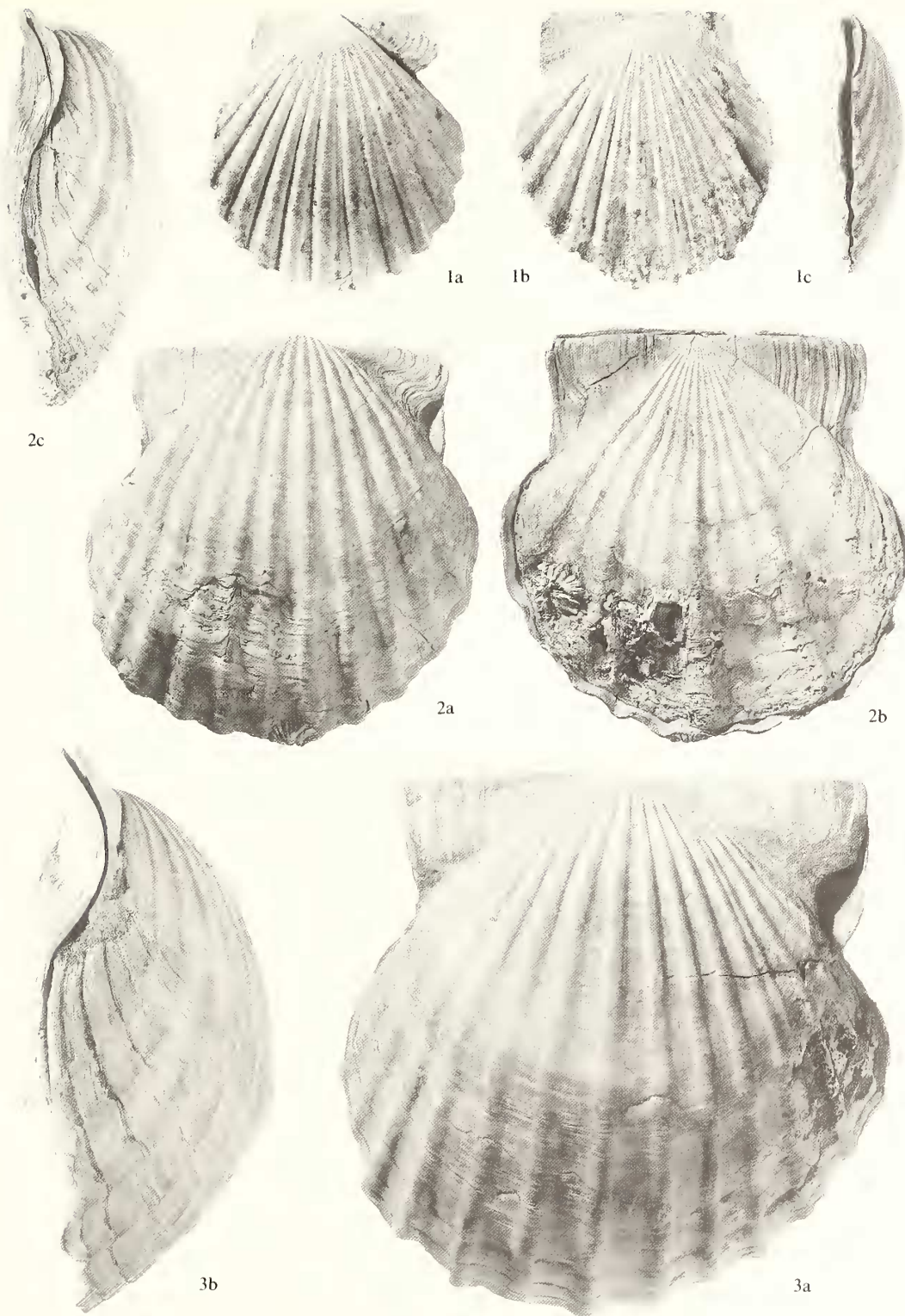
As pointed out by Fukutomi (1953) and Raup (1966) a valve of any bivalve species is fundamentally a rapidly expanding spiral tube, the section of which along the demarcation line can be approximated by an equiangular (logarithmic) spiral. The early part of the spiral near the origin, however, is commonly more or less skipped and not represented by the dissoconch. The geometric nature of an equiangular spiral is, in theory, entirely determined by the spiral angle, which is the constant angle between the radius and the tangential line.

The right valve of *F. takahashii* is bowl-like and intuitively shows a much larger spiral angle (or smaller expansion rate) in comparison with that of *P. yessoensis*. It is, however, not necessarily easy to measure the spiral angle of a valve, because the origin of the supposed equiangular spiral is not shown in the vertical section. Therefore, we estimated its approximate value by the following procedure (see also text-fig. 6).

1. Using a three-dimensional digitizer we obtained a line drawing which shows a perpendicular projection of the top of a radial costa nearest the demarcation line.
2. Two-dimensional co-ordinates with arbitrary axes were determined for more than twenty points (including the beak and a point on the ventral margin) on the line drawing.
3. Using a microcomputer, the best-fit equiangular spiral for these points was determined by the least-square method, and its origin, expansion rate, and spiral angle were calculated.

EXPLANATION OF PLATE 40

Figs. 1-3. *Fortipecten takahashii* (Yokoyama, 1930). 1a-c, young individual (swimming stage), UMUT CM18116a, $\times 1$. 1a: right view, 1b: left view, 1c: posterior view. Loc.: Pliocene Horokaoshirarika Formation at the river floor of the Horoshintachibetsu, Numata Town, central Hokkaido. 2a-c, middle-aged individual showing relatively strong convexity of right valve, UMUT CM18116b, $\times 0.65$. 2a: right view, 2b: left view, 2c: posterior view. Loc.: the same as above. 3a, b, middle-aged individual showing a prosoclineal disc and abrupt inward bending of right valve, UMUT CM 18117b, $\times 0.65$. 3a: right view, 3b: posterior view, Loc.: the same as Plate 39, fig. 1a-d.



As shown in the computer graphics (text-fig. 6), the actual curve of the outer surface in the right valve of *F. takahashii* (and also *P. yessoensis*) can be well approximated by some part of an equiangular spiral, though considerable deviation may occur near the inner bending point in *F. takahashii* and in the latest stage of *P. yessoensis*. The spiral angle (or expansion rate) is remarkably different between the two species. The result of our calculations on a few right valves of each species indicates that the average spiral angle is about 56° in *F. takahashii* but only about 33° in *P. yessoensis*. The profile of an adult right valve of *F. takahashii* looks semicircular not only in vertical section but also in transverse section. In other words, the valve looks hemispherical, because the early part of the expanding tube is largely skipped.

As observed in the samples In and Tk of *F. takahashii*, the extent of surface curvature seems to vary greatly among individuals. Some specimens are of considerable size and relatively weakly inflated, while there are some small specimens with strong convexity (e.g. Pl. 40, fig. 2a-c). The remarkable variation of convexity may be partly due to the variability of the spiral angle but, we suppose, largely attributable to the difference in the extent of skipped portion near the origin of an equiangular spiral. It is a general tendency that an individual with a large skipped portion can grow to a large ultimate size.

Nevertheless, the surface curvature of the young right valve is not much different between *F. takahashii* and *P. yessoensis*. The curvature becomes weaker much more slowly with growth in *F. takahashii*. Such a hemispherical shape of the lower valve is probably advantageous for a stable reclining attitude against water currents and biological disturbance from any direction.

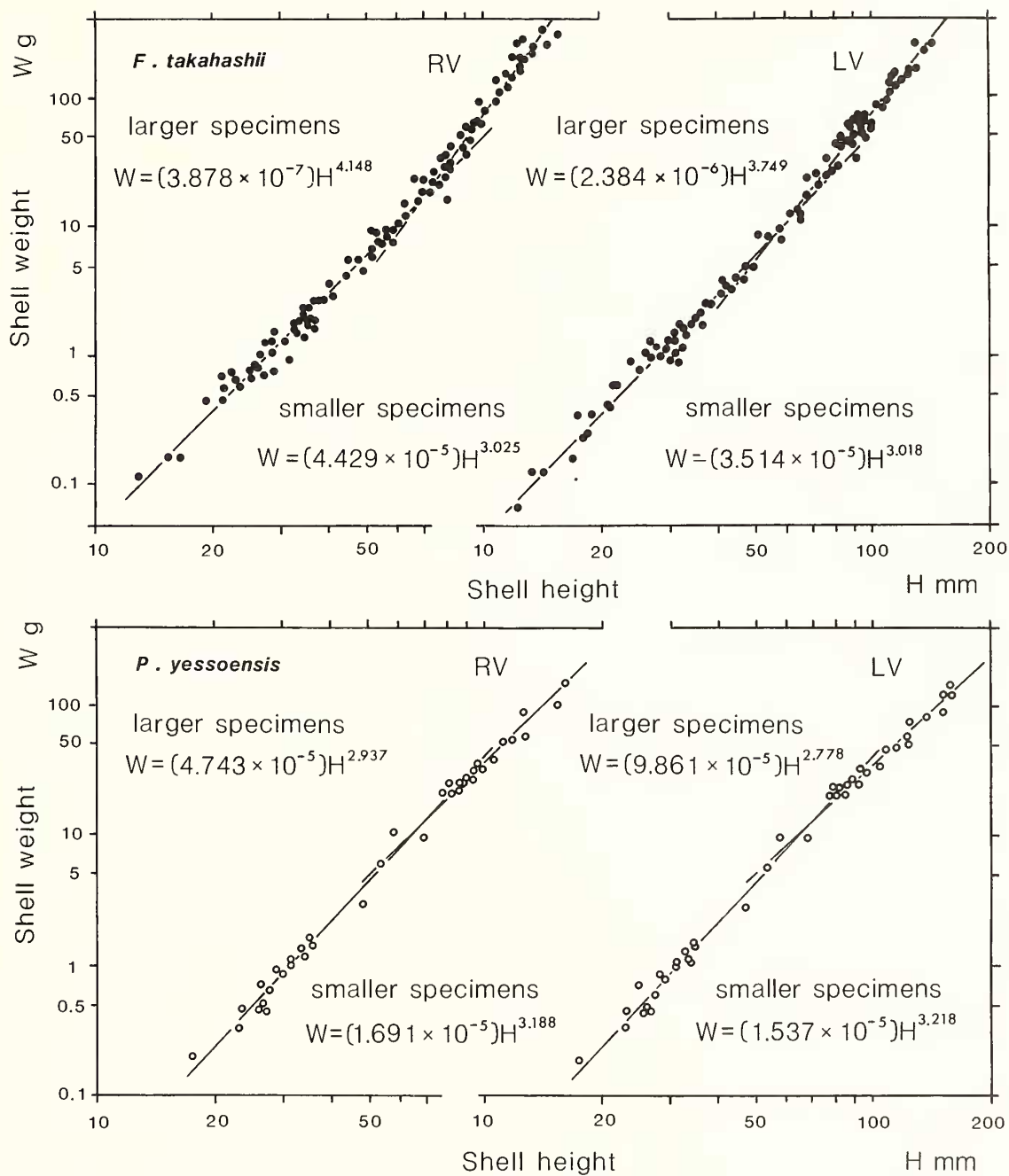
Shell thickness and weight

Because isometric growth of pectinid valves has to result in a steady decrease of the ratio of lift/gravity (Gould 1971), relative thinning of the shell will be particularly effective in maintaining swimming ability until the later growth stages. Jefferies and Minton (1965, text-fig. 10) suggested such a negatively allometric growth of shell thickness to shell size in *Bositra buchi* from the Jurassic, which was regarded by them as a nekto planktonic bivalve. Tanabe (1973) also documented a significantly negative allometry of the thickness of the outer prismatic layer to the shell height in *Sphenoceramus naumanni* and the early growth stages of *S. schmidtii*, for both of which a pseudoplanktonic mode of life was suggested. Though we are not aware of any well-documented biometric study treating this problem with extant pectinids, it would not be surprising if there were a marked difference in the growth patterns between byssate and swimming species.

The thickness of a pectinid shell, however, is somewhat difficult to measure with accuracy, because, even in a vertical section, it is strongly influenced by the radial costation, and because comparison of different individuals at a homologous point is not easy. In the circumstances we examined the allometric relation between shell size (height in this case) and shell weight in each valve. Because weight generally scales at the cube of size, isometric growth will be shown by a growth ratio of 3.

The results of our bivariate analyses are collectively shown in text-fig. 7, which indicates considerably different modes of allometric growth between *F. takahashii* and *P. yessoensis*. In *F. takahashii* the relative growth can be approximated by diphasic allometry; that is, in the early stages it is nearly isometric, whereas in the later stages it evidently turned to positive allometry. This change is observable in both valves. As shown in the vertical section (text-fig. 5), the outer layer and myostracum become suddenly thicker and the accumulation rate of the inner layer must become much larger after the middle stage. Though some artificial division of growth stages is inevitable to analyse the diphasic nature, the calculated growth ratios in Sample In are significantly different between the smaller ($H < 70$ mm) and larger ($H > 70$ mm) individuals (3.025 ± 0.052 and 4.148 ± 0.125 for the right valve, and 3.081 ± 0.051 and 3.749 ± 0.127 for the left valve, respectively). We presume that the more drastic change of growth pattern in the right valve is related to the surface bending in the middle stage, but the relative thickening of the shell with growth is obvious in both valves of *F. takahashii*.

In *P. yessoensis* the relative growth can also be regarded as diphasic, but the direction of change



TEXT-FIG. 7. Allometric relation between shell height (H) and shell weight (W), which indirectly indicates the ontogenetic change of relative shell thickness. In the later stages the shell becomes relatively much thicker in *Fortipecten takahashii* but slightly thinner in *Patinopecten yessoensis*. The scale of abscissae is three times larger than that of ordinates.

is just the reverse. Though the calculated growth ratios are slightly larger than 3 in the early stages of Sample Ak, relative thinning of the shell seems to occur in the later stages. If shell length (L) is applied as a variable for shell size, more obvious negative allometry will be concluded. In conclusion, the growth pattern of *P. yessoensis* seems to reduce the swimming difficulty in the later stages, whereas in *F. takahashii* the relative shell thickening indicates rapid loss of swimming potential after the middle stage.

Obliquity, size, and position of adductor muscles

Thayer (1972) pointed out that the oblique orientation of adductor muscles (especially the longitudinal axis of the striated portion) to commissure plane is a functionally meaningful structure in swimming pectinids, because it enables quicker clapping motion of valves. He studied the obliquity in various free-living and attached species of monomyarian bivalves, and ascertained an intimate relation between this feature and swimming ability; that is, the obliquity is generally large in adept swimmers such as *Amusium japonicum* and *Placopecten magellanicus* but very small in byssate and cemented species. Moreover, in *Himmites multirugosus* it was said that the striated muscle is notably oblique in the early (free-living) stages but almost perpendicular in the later (cemented) stages.

In all the growth stages of *Patinopecten yessoensis* and early stages of *F. takahashii*, as partly shown in text-figs. 5 and 8, the striated muscle is certainly oblique (more than 15° as measured in a plane normal to the hinge) like many other swimming pectinids. In the later stages of *F. takahashii*, however, the obliquity becomes almost zero.

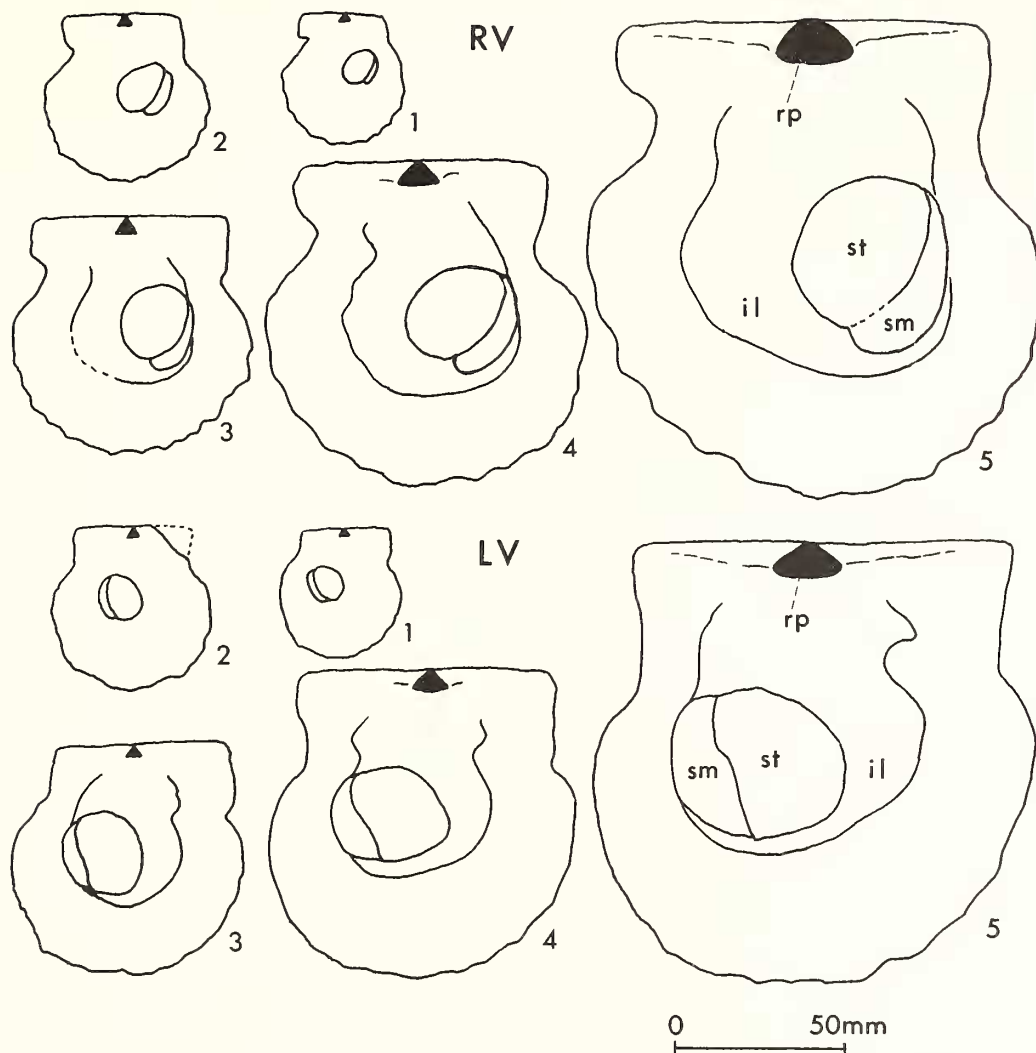
The ontogenetic change of the size and position of striated muscle must be also important in relation to swimming mechanics. As interpreted by Gould (1971), an allometric enlargement of striated muscle and its dislocation from a posterodorsal to a more central portion of the disc, which are observable in *Placopecten magellanicus* and some other free-living pectinids, seem to result in a more powerful clapping motion and reduce the difficulty of swimming in the later stages. Such an improvement of musculature actually occurs in *Patinopecten yessoensis* and probably in the early stages of *F. takahashii*. However, relative enlargement of the smooth portion (instead of the striated portion) seems to occur in the later stages of *F. takahashii* (text-fig. 8). The massive smooth muscle in adult individuals of this species must have produced strong tension in holding the valves tightly closed, which is probably more necessary for a reclining life.

Incidentally, remarkable relative enlargement of smooth muscle occurs in *Chesapecten jeffersonius* from the Pliocene beds around Chesapeake Bay (Gould 1971). Because the adult valves of such large species of *Chesapecten*, described by Ward and Blackwelder (1975), are often as heavy as those of *F. takahashii*, swimming ability may have been completely lost in the later stages, as assumed by Gould (1971) and Miyazaki and Mickevich (1982). The shell form of *Chesapecten*, however, is nearly equiconvex throughout growth and much different from that of *F. takahashii*.

Allometric change of some other characters

In pectinids, as studied by Trueman (1953), the central non-calcified portion of the resilium (inner ligament) serves to open the valves by its compressive elasticity, when the contractional force of the adductor muscles is released. Therefore, it may be natural that thick-shelled pectinids generally require a larger resilium than thin-shelled pectinids of similar size. The relative size of resilial insertion appears to be nearly equal between *P. yessoensis* and *F. takahashii* in their early stages. In adult specimens of *F. takahashii*, however, it becomes unusually large in response to the relative thickening of the valves. The apical angle of the resilial pit is also much widened, and the ratio of its area/valve surface becomes larger in the later stages (text-fig. 8). In *P. yessoensis*, like many free-living and byssate pectinids, the shape and relative size of resilial pit are almost invariant throughout growth.

The ontogenetic change of surface ornamentation is also remarkable in *F. takahashii*. In the early stages the radial costae are commonly simple and subequal in prominence like many species of *Patinopecten*. In the later stages, however, the costae becomes relatively narrower (almost



TEXT-FIG. 8. Ontogenetic change of muscle insertions and resilium pit in *Fortipecten takahashii*. The smooth portion of the adductor muscle and resilium pit become relatively large with growth. re: resilium pit, st: striated portion, sm: smooth portion, il: distribution of inner shell layer.

invariant in absolute width) in the right valve and show two orders of prominence in the left valve. In every sample of *F. takahashii* the adult left valve has commonly five strong radial costae, each interval of which has two (rarely one) weaker costae. This arrangement is somewhat similar to that of the Cretaceous genus *Neithea*. In some middle-sized specimens of *F. takahashii* there are small openings at the ventral ends of these five stronger costae, though their function is unknown.

Range of morphological variation

As stated above, it is noticed that the intrapopulational variation of various morphometric characters (e.g. umbonal angle, disc obliquity, shell convexity, and surface curvature) is much broader in *F. takahashii* than in *P. yessoensis*. The reason is not exactly clear, but one possible

explanation is that a reclining life habit does not require such strict design of shell form as a swimming habit.

HABITAT AND GEOGRAPHIC VARIATION OF *F. TAKAHASHII*

F. takahashii has been regarded as a characteristic element of the Pliocene Takikawa-Tatsunokuchi Fauna which was extensively distributed in Hokkaido and the Pacific side of north Honshu (text-fig. 1). This fauna contrasts with the Omma-Manganji Fauna on the Japan Sea side of Honshu (and south Hokkaido), and also with the Kakegawa Fauna on the Pacific side of south-west Honshu (Chinzei 1978, 1986). The three faunas are at least in part coeval. Constituent species of the Pectinidae as well as other molluscs are largely different between them. The Takikawa-Tatsunokuchi Fauna was distributed in south Sakhalin and further north and east, and is regarded as having lived under the influence of cold water currents, though embayment conditions are generally suggested by the sedimentary facies and constituent molluscs.

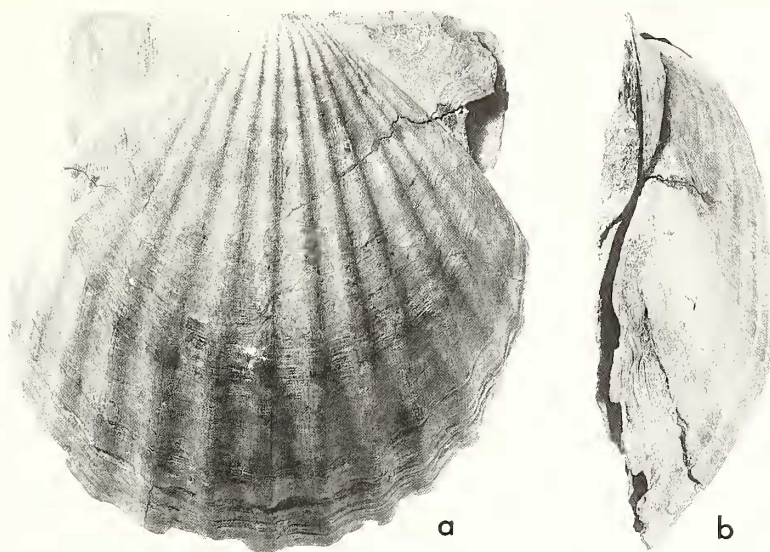
At various localities of Hokkaido and north Honshu *F. takahashii* occurs predominantly in muddy sand. Associated molluscs are generally of low diversity but considerably different between localities. In the Takikawa and Ishikari-numata areas of central Hokkaido, for example, this pectinid is commonly accompanied by *Acila*, *Macoma*, *Mya*, and *Turritella* in one assemblage, and by *Anadara*, *Spisula*, and *Macoma* in another assemblage (Matsui, pers. comm.). In the Sendai Basin (the type Tatsunokuchi Formation) of north-east Honshu, dominant associated molluscs are *Anadara*, *Dosinia*, *Pseudamiantis*, *Peronidia*, and *Neverita* (see Chinzei 1978 for the species names and other details). Burrowing bivalves are generally common, while open sea and rocky shore elements are rarely represented in this fauna. *F. takahashii* seems to have adapted to the muddy sand bottom of shallow bays or inland seas, though it is not clear whether the substrates were soupy or not.

Uozumi *et al.* (1986) studied the stratigraphic range of *F. takahashii* on the basis of various evidence from palaeomagnetism, K-Ar datings and fission-track datings. According to them, this pectinid lived during the greater part of the Pliocene from 6.0 to 2.0 Ma in the Tokachi area on the Pacific side of Hokkaido, but its fossil records disappear much early in the Takikawa and other areas on the Japan Sea side of central-northern Hokkaido, where the Upper Pliocene is commonly represented by non-marine sediments. It is implausible to explain the morphological difference between the Pacific and Japan Sea populations by phylogenetic change. According to Gladenkov (1984) and some other Russian biostratigraphers, this species is also restricted to the Pliocene (mainly lower) in Sakhalin and Kamchatka.

Fortipecten is likely to have been derived from some Miocene stock of *Patinopecten* (*Mizuhopecten*). Though there are a few uncommon and debatable species of *Fortipecten* in the Upper Miocene of Japan and Alaska, the first appearance of *F. takahashii* seems to have been sudden in every examined stratigraphic section. Since the *Gryphaea*-like morphology of this species can be regarded as largely functional, the evolutionary change may have been rapid. It would be futile, therefore, to try to verify the ancestry by finding a gradual morphological change in the fossil record.

As clarified by Suzuki (1979), *F. takahashii* shows a remarkably wide range of geographic variation; the samples from the Pacific sides of Hokkaido and north Honshu (Suzuki's Form B) are characterized by a less inflated right valve and not so heavy shell in comparison with the samples from the Japan Sea side of Hokkaido and Sakhalin (Suzuki's Form A or the typical form). The analyses of relative growth in the present paper are based on the samples In and Tk which belong to the Form A, and only the small sample Sd represents the Form B.

F. kenyoshiensis from the Late Pliocene Togawa Formation in north Honshu is characterized by the much weaker convexity of the right valve, so that Chinzei (1960) regarded it as intermediate between *Patinopecten* and typical *Fortipecten*. The relative growth of this species and its taxonomic relation to the weakly inflated form of *F. takahashii* has not been sufficiently studied, but they were probably also almost immobile recliners, because their adult valves are still much heavier



TEXT-FIG. 9. Full-grown individual (Suzuki's Form B) of *Fortipecten takahashii*, showing relatively weak convexity of right valve and large critical size, UMUT CM18118, $\times 0.65$. *a*: right view, *b*: posterior view. Loc.: Pliocene Tatsunokuchi Formation at the river cliff near Yodomibashi Bridge, Sendai City, north Honshu.

than those of various species of *Patinopecten* and other swimming genera. Because abrupt inward bending of the shell commonly occurs at a larger size (about 100 mm in height) (Chinzei 1960; text-fig. 9), it is highly probable that the change of life habit from a swimmer to a full-time recliner was more or less retarded in these forms. The retardation may be natural, if we assume that relatively thin-shelled forms require larger size before the beginning of reclining life, because immobile recliners must resist predators only by the strength of their shells. These relatively thin-shelled forms are not necessarily ancestral to the typical form of *F. takahashii*, because their first appearance seems to be slightly later than that of the typical form.

Yabe and Hatai (1940) and Akiyama (1962) regarded the peculiar morphology of *F. takahashii* and its morphologic difference between sedimentary basins as largely due to some adaptive response to different environments (or ecophenotypic effect in modern views). Ecophenotypic effect is possible but difficult to verify in this case, and we tentatively assume that the dichotomous geographic variation of this species is due to some geographic isolation of populations between the Japan Sea side and the Pacific side.

DISCUSSION OF MODE OF LIFE

Inferred life mode of F. takahashii

Free-living pectinids, as emphasized by Gould (1971), reveal various allometric changes in shell form and musculature, so that swimming difficulty in later growth stages is reduced. Such allometric changes certainly occur in *P. yessoensis*; e.g. the umbonal angle becomes larger and the thickness of the shell is negatively allometric to shell size. *F. takahashii*, on the contrary, seems to be an unusual pectinid, because of (1) the ontogenetic decrease of the umbonal angle, (2) the disappearance of disc gapes along the anterodorsal and posterodorsal margins, (3) the significant relative thickening of the shell, and (4) the relative enlargement of smooth adductor muscle (see also

TABLE 2. Allometric changes of various characters in the later growth stages of *Fortipecten takahashii* and *Patinopecten yessoensis*.

Character	<i>F. takahashii</i>	<i>P. yessoensis</i>
Umbonal angle	Becoming smaller	Becoming larger
Form ratio (H/L)	Becoming larger	Becoming smaller
Size of auricles	Positively allometric	Nearly isometric
Marginal discrepancy	Positively allometric	Positively allometric
Marginal gapes	Almost disappeared	Becoming wider
Disc symmetry	Becoming prosoclinal	Aclinal throughout growth
Shell convexity (RV)	Positively allometric	Slightly positively allometric
Shell convexity (LV)	Slightly positively allometric	Slightly negatively allometric
Shell convexity (CV)	Positively allometric	Nearly isometric
Shell thickness	Positively allometric	Slightly negatively allometric
Shell weight	Positively allometric	Slightly negatively allometric
Size of striated muscle	Nearly isometric	Positively allometric
Size of smooth muscle	Positively allometric	Negatively allometric
Obliquity of muscles	Decreased toward zero	About 15° throughout growth
Size of resilium pit	Positively allometric	Nearly isometric
Radial costae (RV)	Almost invariable in width	Isometrically widened
Radial costae (LV)	Of two orders of prominence	Of a single order of prominence
Individual variation	Comparatively broad	Comparatively narrow

Table 2). Judging from these allometric features, it is concluded that *F. takahashii* was a swimmer only in the early growth stages but became a full-time recliner after the middle stage.

Such a *Gryphaea*-like heavy shell with a bowl-like lower valve seems to be advantageous for a reclining life in the following ways:

1. The centre of gravity of the whole organism lies inside the cavity of the lower valve, so that the reclining life position, even if physically or biologically disturbed, is readily restored to the original state only by gravity.
2. The strongly inflated lower valve is effective in raising the commissure above the sediment surface, when the organism 'floats' on a muddy substrate.
3. Comparatively large and heavy valves are advantageous for safety, because full-time recliners need to resist various predatory and boring organisms without any escape strategy.

The ontogenetic change of *F. takahashii* seems to satisfy these requirements. The adult individual of this species probably attained its stable life position by burying the greater part of the lower valve in a soft (if not soupy) substrate. Epibionts and boring organisms are very common in the left valves (and the marginal part of the right valves) but much rarer in the main part of the right valve of the same articulated individual. According to our rough calculation, even a full-grown individual (e.g. UMUT CM18117a) could 'float' on soft mud, if the specific gravity of the mud exceeded 1.4.

Comparison with some Mesozoic Gryphaea-like homeomorphs

In gross morphology *F. takahashii* resembles, though of course only superficially, some Mesozoic pectinaceans, e.g. *Neithea* from the Cretaceous and *Weyla* from the Lower Jurassic. The plano-convex shells of these two genera, as discussed before (Hayami and Noda 1977), indicate that they were free-lying on soft substrates but probably not so excellent swimmers as living *Pecten* (s.s.). Carter (1972) and Jablonski and Bottjer (1983) also regarded *N. quinquecostata* from the European Chalk as an iceberg strategist. As the result of our observations of some well-preserved specimens of *N. quinquecostata* from the Chalk, *N. texana* from the Comanche Group of the Gulf Coast,

and *W. alata* from the Andean Liassic limestones, the following features also suggest the difficulty of their swimming movements:

1. The outline of *Neithea* and *Weyla* is generally taller than that of extant swimming pectinids. Their umbonal angles are generally small and almost invariable throughout growth.
2. Disc gapes are generally undeveloped in *Neithea* and *Weyla*.
3. The valves of *Neithea* and *Weyla* look generally heavier than those of extant swimming pectinids of similar size. The aragonitic inner layer is often completely lost during the course of fossilization, but it is noticed that the thickness of the calcitic outer layer is usually positively allometric to shell size.
4. The mode of life of these Mesozoic pectinaceans in early growth stages has not been clarified. Yet, it would not be surprising if many immobile recliners smaller and more thin-shelled than *Fortipecten* could have lived on Mesozoic level bottoms, because predation pressure and bioturbation were probably much weaker in comparison with Cenozoic and modern seas.

Among other Mesozoic pectinaceans some large species of *Boreionectes* [= *Maclearnia*], e.g. *B. imperialis asiaticus* from the lower Neocomian of arctic Siberia (Zakharov 1965, 1966) are noteworthy, because they reveal thick plano-convex shells. Their gross morphology is somewhat similar to that of *Fortipecten*, but they are left-convex instead of right-convex. So far as we observed Zakharov's illustrations of some articulated valves, epibionts and boring organisms are common in the right valves but rare in the left valves. The adult individuals of these species were probably also full-time recliners with the left valve directed down.

In the Mesozoic there are a large number of *Gryphaea*-like homeomorphs in various unrelated families. In addition to above-mentioned pectinaceans, for example, *Gervilleioperna* and *Lithioperna* of the Isognomonidae, *Gervillaria* of the Bakevelliidae, *Volvicramus* and *Inoceramus* (only *I. lamarcki* group) of the Inoceramidae, and *Ctenostreon* of the Limidae can be regarded as full-time recliners. These pteriomorphs are generally thick-shelled and share strong convexity of the lower valve and a well-developed posterior wing without any strong ornamentation. The large posterior wing possibly acted as a stabilizer for maintaining a reclining attitude much as the large auricles of *F. takahashii*.

The morphology and evolutionary change of Liassic *Gryphaea* in western Europe have been studied by a number of authors. As recognized and experimented upon by Zeuner (1933), the narrow and tightly-coiled shell of *G. arcuata* from the Lower Lias is most stable on soft substrates when the left valve is directed down with a nearly horizontal commissure plane. Hallam (1968), having opposed Trueman's (1922) classical orthogenesis theory, considered that the Middle and Upper Liassic bowl-like and relatively thin-shelled species, *G. gigantea*, was derived from the Lower Liassic species through an intermediate species. He interpreted that the evolution was probably promoted by natural selection, because the bowl-like form is more stable against a strong water current of any direction than a narrow and tightly coiled form. The gross morphology of *G. gigantea*, as well as that of *G. dilatata* from the Upper Jurassic, is interestingly similar to the discs of *F. takahashii*. They are commonly characterized by the nearly uniform thickness of the shell with thickly accumulated inner layer and broadly rounded surface of the lower valve. Their hemispherical appearance is due to the growth pattern approximated by a large-angled logarithmic spiral, the early part of which is largely omitted. This can be regarded as approximate to the Rudwickian paradigm which is the most advantageous for an immobile reclining life habit.

Rarity of reclining bivalves in Cenozoic seas

The increase of predation pressure with geologic time (especially after the Mesozoic) and its impact on the course of marine organic evolution are an interesting subject in palaeobiology (Vermeij 1977, 1983; and others). As was discussed by him, armoured strategy is common in gastropods but seems to be rare in bivalves (except for some cemented and byssate genera in warm seas). Almost all the extant bivalves on level bottoms are very large, cryptic, endobysate, or mobile (burrowing, jumping, or swimming). It is, however, plausible that *F. takahashii* alone succeeded

in a reclining life by forming robust valves after the middle growth stage. How rare are reclining bivalves in the Tertiary? Though we have not carried out an exhaustive study of this problem, bowl-shaped bivalves appear to have become much rarer after the Cretaceous. Only *Hinnites crispus* from the Pliocene of Italy, as was interpreted by Seilacher (1984), may have been a secondary recliner after the cemented stage.

In the Tertiary there was a remarkable radiation of a plano-convex group of the Pectinidae, which comprises *Pecten*, *Flabellipecten*, *Oppenheimiopecten*, and *Euvola* (Fleming 1957; and others). The escape behaviour of some extant species of this group was observed by several authors (Dakin 1909; Baird and Gibson 1956; Rees 1957; Baird 1958; Stanley 1970; Thomas and Gruffydd 1971) and also by us in aquaria. Their swimming ability probably declines with growth as a result of lift/gravity relation, and the gerontic individuals of large species may be almost immobile. They may no more need to swim if the smooth adductor muscle grows powerful enough to resist the shell-opening force of starfish which are generally regarded as natural enemies. Lethal boring by naticids and other organisms seems to be rare in the shells of the extant and fossil pectinids treated in this study.

The reclining mode of life of *F. takahashii* may be basically similar to that of the gerontic stage of large species of *Pecten*. Yet the most distinguished peculiarity of *F. takahashii* is that the change of life mode from swimming to reclining seems to have occurred at an unusually young growth stage and, what is more, is well represented by the adaptive morphology. So far as we observed a number of specimens of *P. albicans* from Japan and *P. maximus* from England, the disc gapes are persistent throughout growth, and the relative shell thickening does not occur until the latest stage.

Provided that the swimming velocity of pectinids is independent of shell size (Gould 1971), the swimming potential seems to be indicated by the ratio of surface area/weight, because the lift is considered to be dependent upon the surface area. For simplicity, the surface area is substituted by $L \times H$ (in cm^2), and the soft part is assumed to be equal to the sea water in specific gravity. According to our rough calculation of $L \times H/W$, the ratio rarely falls below 1.0 even in the gerontic individuals of large species of *Patiniopecten* and *Pecten*. In *F. takahashii*, however, the ratio falls below 1.0 in the middle stage (about 70–80 mm in shell height) and becomes 0.4 or still smaller in the full-grown individuals.

There is no positive evidence to assume that the habitat of *F. takahashii* was under a special condition with low predation pressure. It is, however, noteworthy that the associated molluscan fauna is always of unusually low specific diversity and that this exceptional pectinid appeared in

Shell height	0mm	50mm	100mm	150mm
<i>Fortipecten takahashii</i> (strongly inflated form)	Bys.	Swimming	Reclining	
<i>Fortipecten takahashii</i> (weakly inflated form)	Bys.	Swimming	Reclining	
<i>Patiniopecten yessoensis</i>	Bys.	Swimming		
<i>Pecten albicans</i>	Bys.	Swimming		

TEXT-FIG. 10. Diagram showing the relation between shell size (height) and life habits in *Fortipecten takahashii* and two extant swimming species. Bys: byssate stage, the limit of which is estimated by the disappearance of active ctenolium.

some cold-water embayments of the north-western Pacific region. From various evidence it is generally supposed that shell-crushing predators are abundant in tropical shallow seas but less common in cold seas.

CONCLUSION: A RESURRECTION OF MESOZOIC-TYPE RECLINING LIFE

Except for some sedentary species of *Hinnites*, few extant pectinids seem to show such a remarkable allometric change of the dissoconch as *F. takahashii*. Judging from the result of our biometric analysis and various other evidence, it is strongly suggested that this bizarre pectinid abandoned a swimming strategy in the middle growth stage and took an iceberg strategy on soft substrates. Remarkable relative thickening of the shell and common inward bending of each valve, which indicate the abrupt change of life mode, occur at this stage, when the shell height reaches about 70 mm in the strongly inflated typical form from the Japan Sea coast (about 100 mm in the less inflated form from the Pacific coast).

The critical size indicating the strategic change is inversely correlated to the convexity of the right valve not only geographically but also within one and the same sample. In Sample Tk, for instance, adult individuals with large critical size generally show weak surface curvature and relatively thin shells. On the contrary, individuals with strong curvature seem to be characterized by thick shells and relatively small critical and ultimate size. Therefore, the heaviest individual is not necessarily the largest individual. The relationship between the heaviness and convexity may have been controlled by some ecological factor, presumably by the buoyancy of the right valve on soft mud. Although the ancestry of *F. takahashii* is unknown, its geographic and intrapopulational variation seem to suggest that the iceberg strategy was developed at first in the gerontic stage and then phyletically accelerated to the middle growth stage.

The abundance of *F. takahashii* and its related species in the Pliocene (partly also Late Miocene) seas of the north Pacific region can be regarded as an exceptional resurrection of a Mesozoic-type reclining life. Such bowl-like heavy valves with a low centre of gravity seem to guarantee a stable living attitude against physical and biological disturbances, as already tested by *Gryphaea* and many other cup-shaped genera in the Mesozoic. In most Mesozoic homeomorphs it is believed that the reclining stage followed directly the byssate or cemented stage. Their reclining life appears to have initiated at a much smaller size in comparison with *F. takahashii* which overcame the preying danger in the young stages by swimming. Cainozoic level bottom, in general, must have been a much severer environment for recliners than in the Mesozoic, because of the stronger predation pressure and increased bioturbation by deposit feeders. *Fortipecten* succeeded once in developing the iceberg strategy in some cold-water embayments of the north Pacific region, but the success did not continue long, as it became extinct by the beginning of the Pleistocene.

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